

MORPHOLOGICAL DEFINITION OF THE *GUTIERREZIA* GROUP
(ASTERACEAE: ASTEREA)

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ABSTRACT

A putatively monophyletic group of genera related to *Solidago* (*Gutierrezia*, *Gymnosperma*, *Thurovia*, *Amphiachyris*, *Bigelowia*, *Euthamia*, and *Xylothamia*) identified by molecular studies can also be recognized by a specialized morphological feature. The white rayed genus *Gundlachia* is added to this group on the basis of its overall morphology. The anther filaments of these taxa are inserted at the junction of the corolla tube and limb rather than well below the tube apex, as is most common in other Astereae. *Solidago sphacelata* Raf. and *S. discoidea* Ell., which have been segregated as the monotypic genera *Brachychaeta* and *Brintonia*, respectively, also have the distinctive tube-limb filament insertion. In habit, vestiture, leaf morphology, and capitulescence, however, these species, as well as their closest relatives, lie securely within the genus *Solidago*. The subtribe Solidagininae, which comprises the *Gutierrezia* lineage, *Solidago*, *Chrysoma*, and genera of the *Petradoria* group, is recognized by characteristically flat topped capitulescences, primarily yellow rays, and particularly by the distinctive morphology of the disc style appendages.

KEY WORDS: *Gutierrezia*, *Solidago*, *Brachychaeta*, *Brintonia*, *Gundlachia*, Asteraceae, Astereae, Solidagininae

The studies by Suh (1989) and Morgan (1990) of restriction site variation in chloroplast DNA of North American Astereae have identified two closely related groups of genera that have been designated as the "*Solidago* L. lineage" and "*Gutierrezia* Lag. lineage" (Nesom *et al.* 1990). Together, they comprise what can now be relatively clearly defined as the subtribe Solidagininae Hoffm. These plants, in turn, are most closely related within the tribe to the *Aster* L., *Heterotheca* Cass., and *Machaeranthera* Nees lineages, with the *Chrysothamnus* Nutt., *Baccharis* L., and *Erigeron* L. lineages yet more basal in phylogenetic position.

In an effort to identify morphological correlates of these major groups within the tribe, a detailed morphological survey has been conducted, encompassing over 320 species, including 80 American genera of Astereae and many of their subdivisions. Flowers and fruits of each species studied have been dissected and mounted on permanent slides. All vouchers are from LL,TEX; a list of these is deposited in the "*Gutierrezia* reprint folder" at TEX. All species of the North and Central American genera of the *Gutierrezia* and *Solidago* lineages discussed in the text have been studied in detail, except for the following: *Euthamia* (Nutt.) Nutt. ex Cass. (4 species), *Gundlachia* A. Gray (2 species), *Gutierrezia* (5 species), *Solidago* (16 species), and *Stenotus* Nutt. (4 species).

The Solidagininae *sensu stricto* possess a set of features that distinguish them from other Astereae: ray flowers few (or absent), with short, primarily yellow ligules, disc corolla lobes deeply cut, spreading-reflexing, and a uniseriate pappus. Further, the collecting appendages of the disc flower styles have a distinctive, diagnostic, but previously unrecognized morphology: the appendages vary in length (absolutely as well as relative to the stigmatic portions) but the sweeping hairs are more densely arranged than in related lineages of Astereae. The most proximal sweeping hairs are often long-spreading, sometimes appearing like a basal "tuft," but they are quickly reduced in length toward the apex, where they are typically no more than papillate extensions. Some species within *Gutierrezia*, *Xylothamia*, and *Tonestus* have linear appendages with consistently longer sweeping hairs, but these appear to be specializations within the group. The style appendages in the *Machaeranthera*, *Aster*, *Heterotheca*, and *Chrysothamnus* lineages have more widely spaced sweeping hairs that continue to the very apex relatively unreduced in length.

The morphology of the style branches of the bisexual disc florets has been considered to be one of the four defining features of the tribe Astereae (Grau 1977, p. 540). "Style branches are in cross section semi-orbicular and tipped with subulate to triangular appendages covered with collecting hairs. The basal part of these branches is margined with stigmatic lines." And (p. 541) "The only significant variation is in the length of the apical appendage, which may vary from shortly triangular to filiform." In the present paper, I present the first of two major disagreements with Grau's assertion that there is essentially no deviation among styles in the tribe.

The chromosome number of all the plants related to *Solidago* is on a base of $x = 9$, except for *Gutierrezia* and three other genera closely related to it: *Gutierrezia* ($x = 4$ and 5), *Gymnosperma* Less. ($n = 8$, probably based on $x = 4$), *Thurovia* Rose ($x = 5$), and *Amphiachyris* (DC.) Nutt. ($x = 4$ and 5).

The genera of the *Solidago* lineage are the following: *Solidago* (tentatively including *Brintonia* E. Greene, *Brachychaeta* Torr. & Gray, *Oreochrysum** Rydb., and *Oligoneuron* Small) and the genera of the "*Petradoria* group":

*Tonestus** A. Nels., *Stenotus*, *Petradoria** E. Greene, *Vanclevea* E. Greene, *Hesperodoria* E. Greene, *Eastwoodia** Brandeg., *Amphipappus** Torr. & Gray, *Acamptopappus** A. Gray, and *Columbiadoria* Nesom. Those taxa with an asterisk were identified as a monophyletic group in the molecular studies of Suh (1989) or Morgan (1990) or both; the others are added here on the basis of their morphological similarity. Additional comments regarding most of these genera and their morphological coherence are found in a companion paper to this one (Nesom 1991). The genus *Chrysoma* Nutt. is related to *Solidago* but its phylogenetic position is anomalous and discussed separately below. Additionally, the Solidagininae may need to be broadened to include a group of white rayed taxa currently treated within *Aster* L. sensu lato but that appear to be more closely related to *Solidago* (Nesom in prep.).

The studies by Suh (1989) and Suh & Simpson (1990), which were focused primarily on *Gutierrezia*, identified a monophyletic group of genera that constitute the *Gutierrezia* lineage: *Gutierrezia*, *Gymnosperma*, *Thurovia*, *Amphiachyris*, *Bigelowia* DC., and *Euthamia*. Additionally, a group of eight species formerly placed within *Ericameria* Nutt. was segregated as the genus *Xylothamia* Nesom *et al.* (Nesom *et al.* 1990), which is most closely related to *Euthamia* and a part of the *Gutierrezia* lineage. *Gutierrezia*, *Gymnosperma*, *Amphiachyris*, and *Thurovia* have been recognized by various authors as closely related (*e.g.*, Shinnery 1950; Ruffin 1974; Suh & Simpson 1990). Lane (1982) also recognized the relationship and sharply refined the naturalness of the group by excluding the genus *Xanthocephalum* Willd.

One additional genus is added here to the seven identified by Suh as members of the *Gutierrezia* lineage: *Gundlachia* A. Gray, which comprises 6-7 species, all restricted to the Caribbean islands. Its species belong with the *Gutierrezia* lineage in every morphological respect except the color of its rays, which are white, probably as an evolutionary specialization from a yellow rayed ancestor (see below). Upon drying, the ray corollas of *Gundlachia* are more or less the same color as yellow-rayed taxa within the *Gutierrezia* group. *Thurovia* and several species of *Gutierrezia*, as well as species within *Solidago* and *Tonestus*, are also white rayed. The leaf anatomy of *Gundlachia* was observed by Anderson & Creech (1975) to be similar to that of *Euthamia*.

The results of the present morphological survey of American Astereae corroborate Suh's conclusions based on molecular data in regard to the taxa related to *Gutierrezia*. In addition to their molecular similarity, the genera of the *Gutierrezia* lineage have disc corollas shaped more or less like wine glasses, the limb expanding abruptly above the tube, with the anther filaments inserted at the junction of the tube and limb. This feature was documented by Kapoor & Beaudry (1966), who used it to justify the generic segregation of *Euthamia* and *Brachychaeta* Torr. & Gray (see below) from *Solidago*, where the filament insertion in many species occurs well below the apex of the tube. Anderson (1970) noted the similarity in this feature between *Bigelowia* and *Euthamia*,

and on the basis of this and other characters, including karyotype (Anderson 1977), he hypothesized that the two genera are closely related. Outside of the *Gutierrezia* group, filament insertion at the tube-limb junction occurs consistently only in some species of *Solidago* (including *Brachychaeta*, see below), which were not included in Suh's sample, and some taxa of the subtribe Baccharidinae.

Plants of the *Gutierrezia* lineage also are distinguished from those of the *Solidago* lineage by their glabrous or glabrate vestiture (excluding glands), shorter, more elliptic cells of their disc corolla throats, shorter disc style branches and collecting appendages, and a tendency for reduction of the pappus. The pappus is formed of capillary bristles in *Gundlachia*, *Bigelowia*, *Euthamia*, and *Xylothamia*, but in the other genera, which have a reduced chromosome number, the pappus is highly modified or reduced to a crown or series of short scales. In this group of specialized taxa, the disc corolla lobes are also more shallowly cut than in the other genera. Most plants of the *Gutierrezia* lineage have trinerved, punctate glandular, and commonly glutinous, leaves, as do some taxa within the *Solidago* lineage. The capitulescence in the *Gutierrezia* lineage is characteristically flat topped, strongly so in most of the taxa, often with the heads in small glomerules; this is also true within *Solidago* and some genera of the *Petradoria* group. Within the Solidagininae, the heads of relatively dense, flat topped capitulescences tend to open simultaneously and cannot technically be referred to as either cymoid or corymboid. In fewer flowered capitulescences, such as in some genera of the *Petradoria* group, the heads are clearly in a cymoid arrangement. Nevertheless, it seems likely that all flat topped capitulescences in the subtribe are homologous. In general, the *Gutierrezia* group is more homogeneous than the *Petradoria* group in capitulescence, head size, leaf morphology, and ray and disc corolla morphology; some taxa of both groups have highly modified pappus, and within both groups variation exists in almost all features.

The relationship of *Brachychaeta* and *Brintonia* to *Solidago*

A position of anther filament insertion similar to that in the *Gutierrezia* lineage occurs in two species sometimes treated within *Solidago*, but each has also been segregated as a monotypic genus: *Brachychaeta* Torr. & Gray (*Brachychaeta sphacelata* [Raf.] Britton = *S. sphacelata* Raf.) and *Brintonia* E. Greene (*Brintonia discoidea* [Ell.] E. Greene = *S. discoidea* Ell.). Both were treated at the generic rank by Kapoor & Beaudry (1966), although they described the filaments of *Brintonia* as inserted below the tube apex.

Solidago sphacelata (*Brachychaeta*) occurs in Kentucky, Virginia, North Carolina, Tennessee, Georgia, and Mississippi. It has been treated as *Solidago* by all recent accounts of the North American flora and by regional floras (e.g.,

Radford, Ahles, & Bell 1968; Cronquist 1980). Even its original authors, Torrey & Gray, observed differences from *Solidago* only in its cordate leaves and very short pappus, which comprises a whorl of bristles 0.5-1.0 mm long but otherwise similar to bristles of typical *Solidago* taxa.

Solidago discoidea (*Brintonia*) occurs across the Gulf coastal plain from Florida to Louisiana. Radford, Ahles, & Bell (1968) treated it as a species of *Solidago*. Cronquist (1980), however, separated it as a monotypic genus, but he provided no rationale for treating it at this rank, nor for consistency did he explain why he maintained *Brachychaeta* within *Solidago*. The heads of *S. discoidea* are eradiate, and the disc corollas are white, commonly with a purple tinge; its other features are typical of *Solidago*, although it produces pappus bristles with dilated apices, which are not common in other species.

On the basis of leaf anatomy, Anderson & Creech (1975) found both *Brachychaeta* and *Brintonia* more similar to "typical" *Solidago* than to any proposed generic segregates of *Solidago*, although *Euthamia* was the only such of the *Gutierrezia* lineage included in their sample. *Brachychaeta* and *Brintonia* also are similar to *Solidago* in their woodland habitat, rhizomatous habit, cauline leaves gradually reduced upwards, relatively thin, eglandular, and net veined leaves with sharply serrate margins, and sparsely pilose vestiture. The heads of *Brachychaeta* are secund on curving branches, while those of *Brintonia* are arranged in a thyrsoid capitulescence; both of these capitular arrangements are common in *Solidago*.

The closest relatives of *Solidago sphacelata* are almost certainly the species of "typical" *Solidago*, *S. brachyphylla* Chapm. and *S. auriculata* Shuttl. ex S.F. Blake. Both of these species have secund flowering branches, cordate lower leaves with margined petioles, and definitely shortened pappus bristles (ca. 2 mm long, half the length of the disc corollas). And significantly, the anther filaments are inserted at the tube-limb junction exactly as in *S. sphacelata*. Fernald (1950) hypothesized that *S. sphacelata* hybridizes with *S. ulmifolia* Muhl. ex Willd., but the latter, while perhaps also closely related, has anther filaments inserted below the tube apex. The two closest relatives of *S. sphacelata*, as hypothesized here, are allopatric with it and apparently do not form natural hybrids.

Solidago discoidea is almost certainly the sister species of the only other white flowered species clearly within *Solidago*, *S. bicolor* L. The latter has a thyrsoid capitulescence, white ray corollas, anther filaments inserted at the tube-limb junction, and pappus bristles with dilated apices. *Solidago discoidea* is set apart in taxonomic rank from this species solely on the basis of its discoid heads, and at least one other species of *Solidago* (*S. brachyphylla*) is eradiate. Many genera of Astereae comprise both radiate and eradiate taxa. *Solidago discoidea* and *S. bicolor* in turn appear to be closely related to the typically yellow rayed *S. macrophylla* Pursh, to which they are otherwise similar in capitulescence, corolla morphology, and pappus. *Solidago caesia* L. also is

similar in capitulescence and disc corolla morphology and probably closely related to these.

The two species groups discussed above (those centered around *Solidago sphacelata* and *S. discoidea*) have similar disc corollas, and they are similar in this respect to at least one other group among the *Solidago* species included in the present survey, the *S. wrightii* A. Gray-*S. petiolaris* Ait. species complex (Nesom 1990), which produce thyrsoid to flat topped capitulescences. This feature of corolla morphology (tube-limb filament insertion), which is invariable within the *Gutierrezia* lineage, also appears to be a reliable marker of species groups within *Solidago*, and in a broader survey of species within the genus, it may prove to be critical in identifying major lineages. In fact, the species of my sample with this feature correspond exactly to one of the two major species groups within *Solidago* identified by Anderson & Creech (1975), those lacking secretory cavities and mostly with bifacial mesophyll.

The status of *Oreochrysum*, *Oligoneuron*, and *Unamia*

Two other yellow flowered generic segregates of *Solidago* have been proposed: *Oreochrysum* Rydb. (monotypic) and *Oligoneuron* Small (ca. 6-8 species). Both of these have a typical *Solidago*-like habit and produce flat topped capitulescences. Because most of the genera related to *Solidago* (those of the *Gutierrezia* and *Petradoria* groups), and yet other infrageneric groups within *Solidago* (e.g., the *S. petiolaris* group), produce similar capitulescences, it can be assumed that this is the primitive form within *Solidago*. The anther filaments of both *Oreochrysum* and *Oligoneuron* are inserted at midtube, and the morphological justification for segregating them taxonomically relies primarily on characters of the phyllaries. Rydberg emphasized the distinctiveness of the long style appendages of *Oreochrysum*, but other species within *Solidago* have similar ones (e.g., *S. macrophylla* Pursh and even the genotype, *S. virgaurea* L.). The phyllaries of *Oligoneuron* are multinerved, but so are they in other species (e.g., *S. hintoniorum* Nesom). Both taxa may be kept within *Solidago* on the basis of morphology, in agreement with Anderson & Creech (1975). The molecular data of Morgan (1990), however, whose sample of the subtribe included three genera, showed *Oreochrysum* more closely related to *Tonestus* than to *Solidago*. The relationship of a third generic segregate, the white flowered *Unamia* E. Greene (*Solidago ptarmicoides* [Nees] Boivin), to *Solidago* is more complex and is considered within part of a separate paper (Nesom in prep.).

The relationship of the *Gutierrezia* and *Solidago* lineages

The discoid heads, shortened pappus, and distinctive filament insertion found in *Solidago sphaelata* and *S. discoidea*, as well as those species putatively related to them, are features otherwise uncommon in *Solidago* but characteristic of the *Gutierrezia* lineage. The style branches and collecting appendages within the genus *Solidago* are mostly short lanceolate to deltate, similar to those found in the taxa of the *Gutierrezia* lineage, while in the remaining genera of the *Petradoria* group, the style branches and appendages are mostly linear. Further, *Thurovia* and occasional individuals of *Gutierrezia texana* (DC.) Torr. & Gray produce secund flowering branches, with the heads all positioned on one side, a feature characteristic of many *Solidago* species. Conversely, several groups of *Solidago* produce distinctly flat topped capitulescences, which are characteristic of most of the other genera of Solidagininae, in both the *Gutierrezia* and *Solidago* lineages. While the vestiture of *Solidago* is in general different from that of its close relatives, at least two species, *S. odora* Ait. and *S. chapmanii* A. Gray, have punctate glandular leaves, although the anatomy of the glands is different from those of the remainder of the Solidagininae (Anderson & Creech 1975). In summary, variability within *Solidago* includes most of the features that characterize the *Gutierrezia* lineage, perhaps providing an indication of the ancestral position of the former with regard to the latter (Fig. 1).

The molecular data of Suh and Morgan, while highly incomplete with respect to the taxa of Solidagininae, contradict an hypothesis that places *Solidago* as potentially ancestral to both the *Gutierrezia* lineage and the remainder of the *Solidago* lineage (the *Petradoria* group) (Fig. 1). The two species of *Solidago* in Suh's analysis (*S. altissima* L. and *S. nemoralis* Ait.), both with a similar capitulescence and midtube filament insertion, form the sister group of the *Petradoria* group, and these two clades in turn are phylogenetically coordinate with the *Gutierrezia* lineage. In future molecular studies, it will be critical to investigate a wider range of species within *Solidago*, since I have found no morphological specialization that could be used to support a closer relationship between *Solidago* and the *Petradoria* group than between *Solidago* and the *Gutierrezia* group.

Solidago is by far the largest genus among its relatives and also the most widespread, with species covering all of North America. It becomes much less common southward and is represented in South America by only a single species, which nevertheless appears to be autochthonous there. *Solidago* sensu stricto also occurs in Europe and Asia, where it is represented perhaps by only one variable species (the genotype) or a small group of closely related ones. The other genera of the *Solidago* lineage (the *Petradoria* group) are primarily confined to western North America. Those of the *Gutierrezia* lineage extend from the Caribbean Islands and eastern North America, to western North

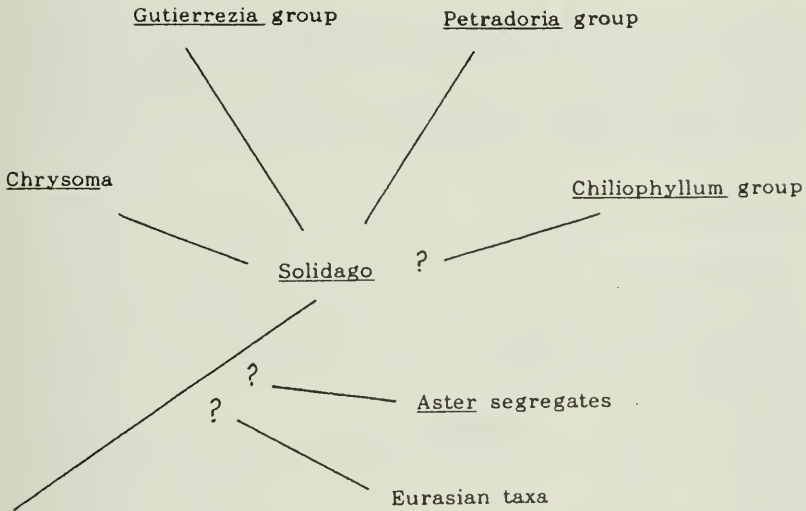


Figure 1. Phylogenetic hypothesis for the subtribe Solidagininae.

America and México. *Xylothamia* and *Gymnosperma* have primarily Mexican distributions. *Gutierrezia* occurs in México and the western United States and has a disjunct group of highly polyploid species in South America (Solbrig 1966).

Solidagininae in South America

A group of closely inter-related genera endemic to South America appears to belong to the Solidagininae: *Chiliophyllum* Phil., *Chiliotrichium* Cass., *Chiliotrichopsis* Cabrera, *Nardophyllum* Hook. & Arn., *Parastrephia* Nutt., and probably *Aylacophora* Cabrera. Several of these genera were included by Hoffmann (1890) in his conspectus of the subtribe. They are all small shrubs with numerous, relatively small heads, yellow flowers, reduced rays, disc corollas with spreading-reflexed or coiling lobes and anther filaments inserted at the tube-limb junction, linear, somewhat "Solidagolike" style appendages, and in some the vascular traces of the style appendages are prominently broadened. The leaves are ericoid, densely tomentose beneath. Punctate glands are produced in a few of the species, but most have numerous, small, epiphyllous glands. There is a strong tendency in several of the genera for the receptacles to produce long pales, and the achenes are often densely glandular. The chromosome number has not been reported for any of the taxa. Apart from

Gutierrezia, these are the only South American taxa that appear to belong to the subtribe, based on their morphology, but the nature of their relationship to the rest of the subtribe is not clear (Fig. 1). The present study is incomplete insofar as it has not taken extra-American taxa into account, but these will be covered as my sample of genera of *Astereae* expands.

The position of *Chrysoma*

Chrysoma, a monotypic genus of the southeastern United States, is a woody shrub that produces small heads in "corymbs," yellow rays reduced in size and number, sometimes completely absent, and deeply cut, spreading-recurved disc corolla lobes. These features and its style appendage morphology place it in the *Solidagininae*, where, however, it is not obviously allied to any of the genera. Greene (1895) enlarged *Chrysoma* to include *Gundlachia*, which is similar in habit and leaf shape, and the geographic position of *Chrysoma* suggests that it would be a member of the *Gutierrezia* lineage. In contrast, the near perfect correlation between the distinctive molecular characteristics and the morphology (particularly the filament insertion and punctate glandular vestiture) of the previously identified members of the *Gutierrezia* lineage suggests that *Chrysoma* is not a part of that group. The anther filaments in *Chrysoma* appear to be inserted at midtube, although the disc corollas are greatly elongated, making the tube-limb transition difficult to identify. The leaf surface is composed of subisodiametric areoles, giving a snake-skin appearance, each areole surrounded by a sunken reticulum that appears to be the source of a resinous exudate. Further, the phyllaries of *Chrysoma* have an orange resinous midvein continuous from base to tip, more similar to those of *Solidago* than to the gland tipped phyllaries of the *Gutierrezia* lineage, and the leaves of *Chrysoma* do not produce storage parenchyma like that found in *Euthamia* and *Gundlachia* (Anderson & Creech 1975). A more precise phylogenetic positioning of this anomalous species awaits further data, but it may have been derived from the ancestral *Solidago*-like complex independently of both the *Gutierrezia* lineage and the genera of the *Petradoria* group (Fig. 1).

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